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Sulfide Shrimp? Observations on the concealed life history of the Thermosbaenacea (Crustacea)

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Abstract

The discovery and subsequent observation over various years of a massive population of the thermosbaenacean *Tethysbaena ophelicola* Wagner in the subterranean karstic sulfide pool of Ayyalon (Israel) enabled us to reach conclusions about the previously unknown life strategy of this crustacean super-order. These are preferably monophagous sulfur-bacteria-eating pelagic shrimps of stratified subterranean pools, adapted to microaerobic-anaerobic conditions, by among others ovoviviparity and the probable help of sulfide detoxifying bacterial endosymbiosis.

Keywords

Thermosbaenacea, Chemoautotrophy, Sulphobacteria, Biospeleology, Ayyalon, Ophel

The frequency of the Thermosbaenacea

The Thermosbaenacea is a super-order of small, blind subterranean crustaceans are routinely mentioned in the same breath with the Speleogriphacea, Mictacea and a host of strange underworld creatures (Olesen et al. 2014). Giere (2009) calls them "rare meiobenthic malacostracans". Iliffe and Kornicker (2008) include them among "living fossil animals", although *Tulumella*, one of their genera, is widespread and common in some West-Indian anchialine cave waters. These crustaceans count today 36 species and are circumtropically distributed.

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The specific biotope of the continental thermosbaenaceans is unknown, or in better terms unreachable and their life history equally hidden. Rich populations of the nominal species, *Thermosbaena mirabilis* Monod resettle the hot bath basins they live in after every disinfection of them, coming from the "interstitial" (see discussion by Barker 1959). *Tethysbaena texana* (Maguire), reported in small numbers in several wells and pumps, is expected to inhabit (Wagner 1994) the whole area of the extensive Edwards Aquifer of Texas, hundreds of meters below ground. *Halosbaena acanthura* was discovered by Stock (1976) in inshore coral rubble in Curaçao and in later samplings, some of which by means of a biophreatic pump, over a wide area extending from Cuba to Colombia in a diversity of habitats. Classical localities of thermosbaenaceans were cave lakes, but it was already early evident that these lakes were not their primary habitat. *Tethysbaena vinabayesi* Wagner, 1994 was encountered during several years in immense numbers in a cave lake in Cuba. After suffering pollution, the crustaceans almost disappeared into the groundwater and only a few individuals could be collected from the detritus on the bottom (Wagner 1994). Several thermosbaenacean species, on the contrary, have been described only from few and damaged specimens spilled-out at spring heads. Such was for instance the case of *Tethysbaena relicta*, which I found in fragments (Por 1962) in the hot spring Hamei Zohar by the Dead Sea in Israel. When later, scattered specimens of the same species were collected in a drift net fixed to the outflow of a major thermo-haline spring, a few hundred kilometers to the north, it became clear that *T. relicta* inhabits the whole groundwater system of the Dead Sea-Jordan Rift Valley aquifer (Dimentman and Por 1991).

With the exception of three or four species which live in marine anchialine caves where they could be reached only by submarine cave divers, thermosbaenaceans were rarely collected and observed in their natural environment (Fryer 1965). They appear in wells, are swept-out in mostly thermal springs, pumped-out from aquifers and interstitial by various devices and occur in spring-fed subterranean lakes. Consequently, species of Thermosbaenacea have mostly been described on the basis of single, often damaged specimens, or in the best of the cases from marginal non-reproducing populations. It was more or less generally accepted that the core populations of these crustaceans are found deep underground in the inaccessible phreatic waters (e.g. Schram 1986). Therefore, even though the external morphology of the Thermosbaenacea has been exceptionally well described, many aspects of their life history of the animals remain hidden. Still, as it will be shown, the Thermosbaenacea are mainly very specialized and probably extremely frequent inhabitants of a very typical kind of subterranean waters, the sulfidic pools.

Only by observing the live animals in their natural environment, the natural history of the Thermosbaenacea can be sketched out. In this review paper I supplement older fragmentary natural history data on preserved or laboratory kept animals with new observations, and propose a consistent life strategy of these unique extremophilic crustaceans (Fig. 1).

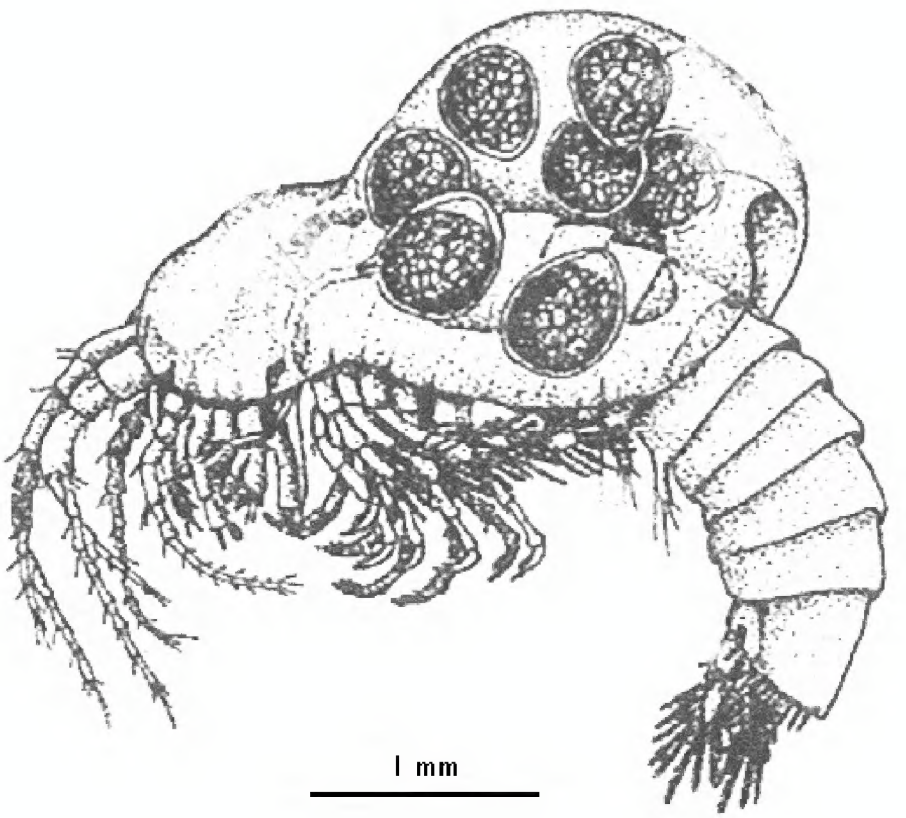

Figure 1. The extremophilic *Thermosbaena mirabilis* Monod from, El Hamma, Tunisia, a little known illustration (Barker 1962).

The core habitat at Ayyalon

The sulfidic and bacteria-rich waters of a subterranean phreatic pool in Israel (Por 2007) which houses a large population of a thermosbaenacean living in its natural environment offered us the opportunity to study the behavior and to understand the functional significance of many characteristic features of these crustaceans. This became possible, when by chance, a system of karstic ducts in the Israeli inner coastal plain became accessible at the bottom of a hundred meter deep limestone quarry (Por 2007, Naaman 2011). It led to a phreatic void containing a deep pool, called in literature the Ayyalon Cave (Fig. 2). This pristine groundwater pool was found to be inhabited among others by an extremely numerous and thriving population of thermosbaenaceans (Por 2007, 2011, 2012), later described as *Tethysbaena ophelicola* Wagner, 2012 (Fig. 3). The fauna of the practically anaerobic, sulfidic and hot pool (Naaman 2011) is probably exclusively based on the chemoautotrophic production of sulfide oxidizing bacteria (Por 2007, Por et al. 2013), even though, in the abundant bacterial mats only *Beggiatoa* sp. has been identified till now. The specimens of *T. ophelicola*, measured slightly more than two mm, well within the average of the super-order. The population of thermosbaenaceans, floating freely in the pond and collected by hand net could reach by my estimate several thousands of individuals by square meter. No particular concentration around the margin of the pond or attraction to the light was noted.

Figure 2. The sulfidic pool of Ayyalon (photo I. Naaman).

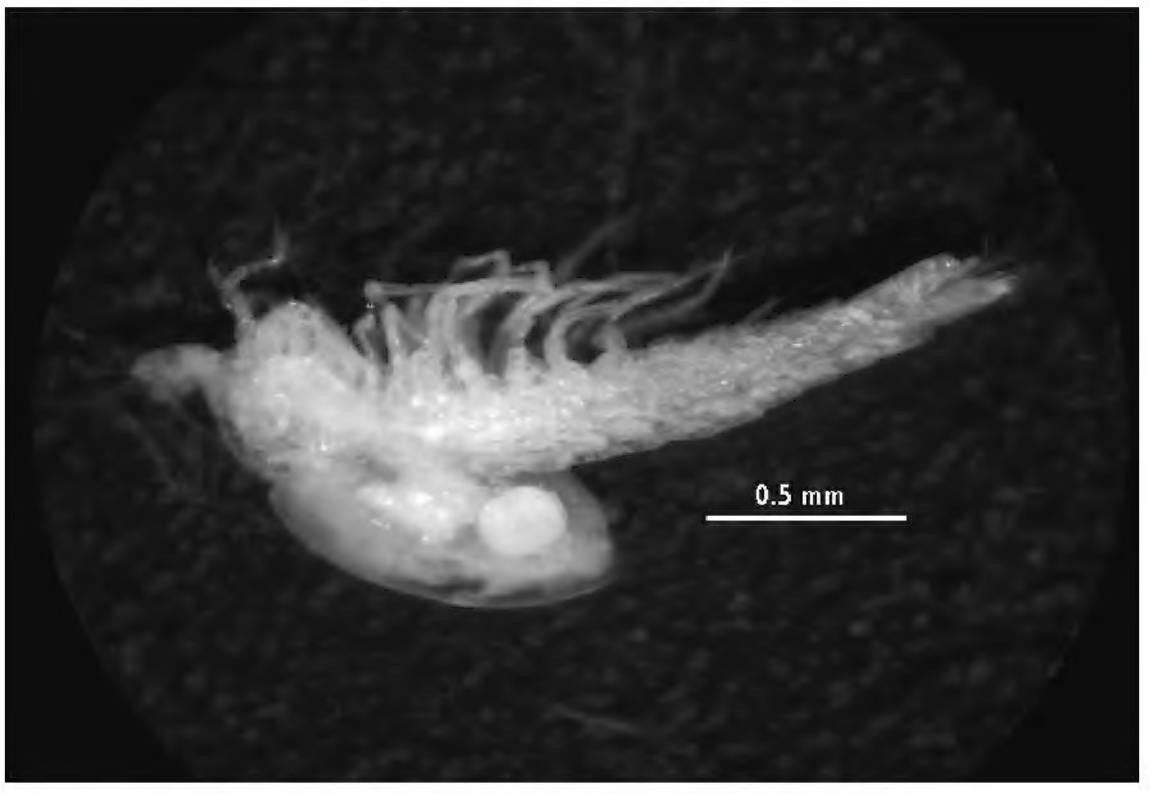

Figure 3. *Tethysbaena ophelicola* Wagner from the sulfidic pool of Ayyalon.

Due to the possibility of observing live populations of *T. ophelicola* in their own aquatic medium over a period of several years many natural history observations could be made, which, I propose can be extrapolated to Thermosbaenacea in general. Most importantly, sulfide bacteria-based chemoautotrophic groundwater ecosystem, called the Ophel biome (Por 2007), is suggested to be much looked for core habitat of the continental thermosbaenaceans.

Hypogene and sulfidic cave systems

The majority of the karstic duct and cave systems are generated by carbonic acid dissolution of horizontally flowing calcium carbonate-carrying phreatic water. However, according to Palmer (2007), some 10% of the caves worldwide are formed by sulfuric corrosion by artesian ascending hydrogen sulfide-carrying phreatic water. The ophelic ecosystems are generated in pools where the ascending anaerobic sulfidic water is contained in the chimneys of hypogene origin (Klimchouk 2007) until reaching oxygene-carrying phreatics or air voids where bacteria oxidize sulfide to sulfate. Sulfidic and hypogene speleogenesis have only recently attracted the attention of the speleologists. For example, Vaxevanopoulos (2009) calculated that 20% of the accessible Greek caves contain hypogenic features. These are ducts which once must have contained aggressive sulfidic water, but are now dried out because of changes that occurred in the water table. It is reasonable to assume that many "active" ducts containing sites like the Ayyalon pool exist deep in the inaccessible aquifers. Some of these are most probably inhabited by *Tethysbaena aiakos* which has been described from various localities in Greece by Wagner (1994), from several damaged specimens swept out to the surface.

Subterranean lacustrine crustaceans

The massive *Tethysbaena ophelicola* population in Ayyalon pool is swimming or floating in the open standing waters of the little lake (Por 2007). Stella (1951) already considered that *Tethysbaena argentarii*, the second species of the super-order to be discovered, is planktonic, but Fryer (1965) declared this observation to be "definitely misleading". Thereafter, in literature the characterization of the thermosbaenaceans prevailed as benthonic animals. Evidently, Stella saw the animals in their Italian subterranean cave, very probably near their native environment. Fryer on the contrary, observed them in Petri dishes after being sent to England. The capacity for occasional swimming of the captured animals though was mentioned by Fryer (1965). The picture would clarify as follows: The Thermosbaenacea are active and gliding swimmers, which despite their millimetric sizes, classify as micronecton rather than plankton. The animals, as shown, clearly prefer floating and swimming to walking. *Ipso facto*, the Ayyalon pool becomes into the first known example of a subterranean lacustrine lenitic environment with biota adapted to life in standing groundwater bodies, a "spelaeopelagial".

The Thermosbaenaceans are able to crawl also awkwardly on the bottom with their pereiopods. This happens normally when the liquid volume is limited or otherwise inadequate. This capacity had to be evidently maintained in their subterranean world in which the lenitic habitat is evidently unstable or when there is a need for the active diffusion of the species.

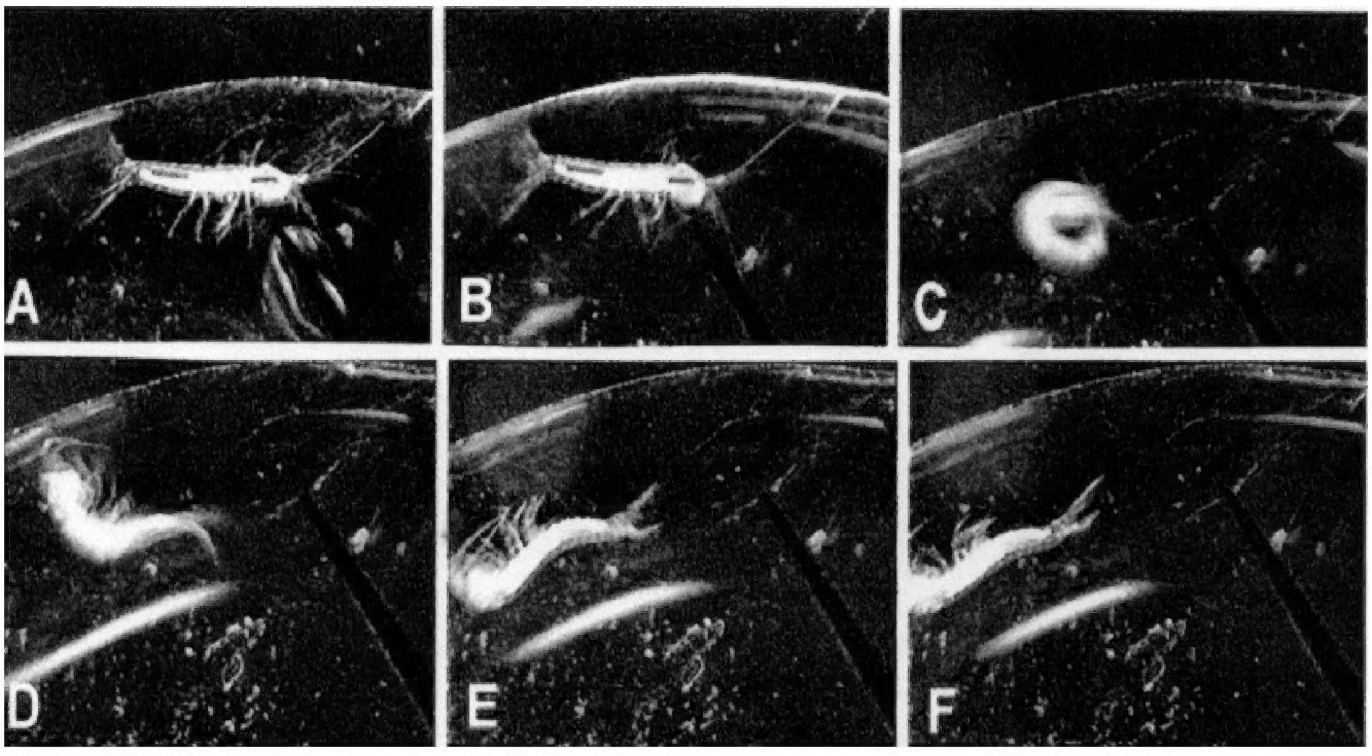

Figure 4. *Tethysbaena argentarii* Stella. Backdown swimming recovery after disturbance (filmed sequence by Olesen et al. 2006).

The meaning of back swimming

Barker (1962) was first to mention that *Thermosbaena mirabilis* swims in an upside-down, notonectic position. Fryer (1965) observed that *Tethysbaena argentarii* swims in inverted position which "recalls an anostracan" often "hanging" motionless on the water surface. The observations in the Ayyalon populations of *T. ophelica* confirmed this type of behavior. The animals were customarily gliding-hovering below the water surface and or on the bacterial crust. While studying the escape behavior of *T. argentarii*, Olesen et al. (2006) observed that the animals returned to the basic notonectic swimming stance after each disturbance (Fig. 4). This is reminiscent of the hyponeustonic life style of some open water crustaceans.

Such a hyponeuston-like behavior permits the thermosbaenacean to maintain itself in the density layer of the redox interphase where the bacteria concentrate. This can be either the surface of the sulfidic pool itself or the pycnocline between the aerobic and anaerobic phreatics. By hovering-floating they can probably adjust to the microlevel where all the composing factors are found in the optimal possible combination for them. Yager (1988) observed that the populations of the anchialine *Tulumella grandis* are concentrated below, or just above and below, the density interface, while Bowman and Iliffe (1988) found *T. unidens* just above the halocline. Possibly though, in the anchialine media, it all depended probably, on the level of the maximum bacterial concentration in the pycnocline of the sulfur and other types bacteria.

The possibility that this super-order uses the mechanical support of water density to glide-on is most probably a considerable energy saving for the animals in the anoxic or microxic, chemoautotrophic media in which they live.

The sulfide shrimp

As they live in a limnetic environment, thermosbaenaceans are characteristically soft-bodied and weakly chitinized. Blood-filled lacunae accompany the integument of the body and of the limbs, providing a diffuse respiratory lacunar system that to a large extent replaces the well-defined vascular respiratory system of other crustaceans (Wirkner and Richter 2009). They can probably relay on gas exchange through the whole body surface, not unlike what meiobenthic animals with similar body mass do in in oxygen poor sediments (Giere 2009). The blood-filled carapace, the pereiopodal exopodites, and the maxillipedes have an especially important respiratory function (Siewing 1958, Barker 1962). Fryer (1965) observed that when the animals are at rest, the maxillipedal epipodites continue beating and with increasing rhythm when oxygen decreases in the water. These mouthparts are especially important in creating a respiratory current which bathes the cavity of the dorsal brood pouch (Zilch 1976).

Observations on the Ayyalon population could not add anything specific and new concerning the physiological aspects of thermosbaenacean anaerobism. There is little doubt that the super-order possesses the arthropodan haemocyanin as its respiratory pigment, like most of the crustaceans. They have a very strong affinity to low oxygen concentrations and are resistant to high temperatures and presence of hydrogen sulfide (Hochachka and Sommers 2000, Grieshaber and Völkel 1998). A West Indian *Tulumella* species is known to use the so called "malate dismutation" of the anaerobic respiration cycle, which produces up to five times more energy than the normal glycolysis (Bishop et al. 2004). It is reasonable to assume that the continental thermosbaenaceans also make use of the malate-improved anaerobiotic respiration which liberates them to a considerable extent from the "oxygen debt".

Hydrogen sulfide is strongly toxic to metazoans (Grieshaber and Völkel 1998). In contradiction, many, if not most of the Thermosbaenacea have been reported from waters where hydrogen sulfide is abundant. Sket (1988, 1996) dedicated much attention to the relationship between the Dalmatian subterranean fauna and sulfidic waters and particularly to *Tethysbaena halophila* (S. L. Karaman, 1953). Wagner (2012) mentioned that anoxic conditions are favorable to Thermosbaenacea and feeding on sulfur bacteria is widespread among them. The massive population of *Tethysbaena ophelicola* at Ayyalon, considered here as the outstanding biotope of the super-order, was found to have H_2S values up to 4.7 mg/l (Naaman 2013). This was the reason for calling them "sulfide shrimp" (Por 2011).

A strong possibility for the way in which the animals cope with the sulfide toxicity is the fact that the specimens of *Tethysbaena* at Ayyalon have their intestinal tract clogged with live bacteria, even in the young instars newly cast from the brooding pouches of the females (Fig. 5). In literature, there are several instances in which thermosbaenaceans are drawn or photographed with dark, full intestines (e.g. *Halosbaena acanthura* in Stock 1976) (Fig. 6). Fryer (1965), when observing live specimens of *Tethysbaena argentarii*, found their gut usually filled from end to end with "unrecognizable material of brownish hinge broken down by the time it became available".

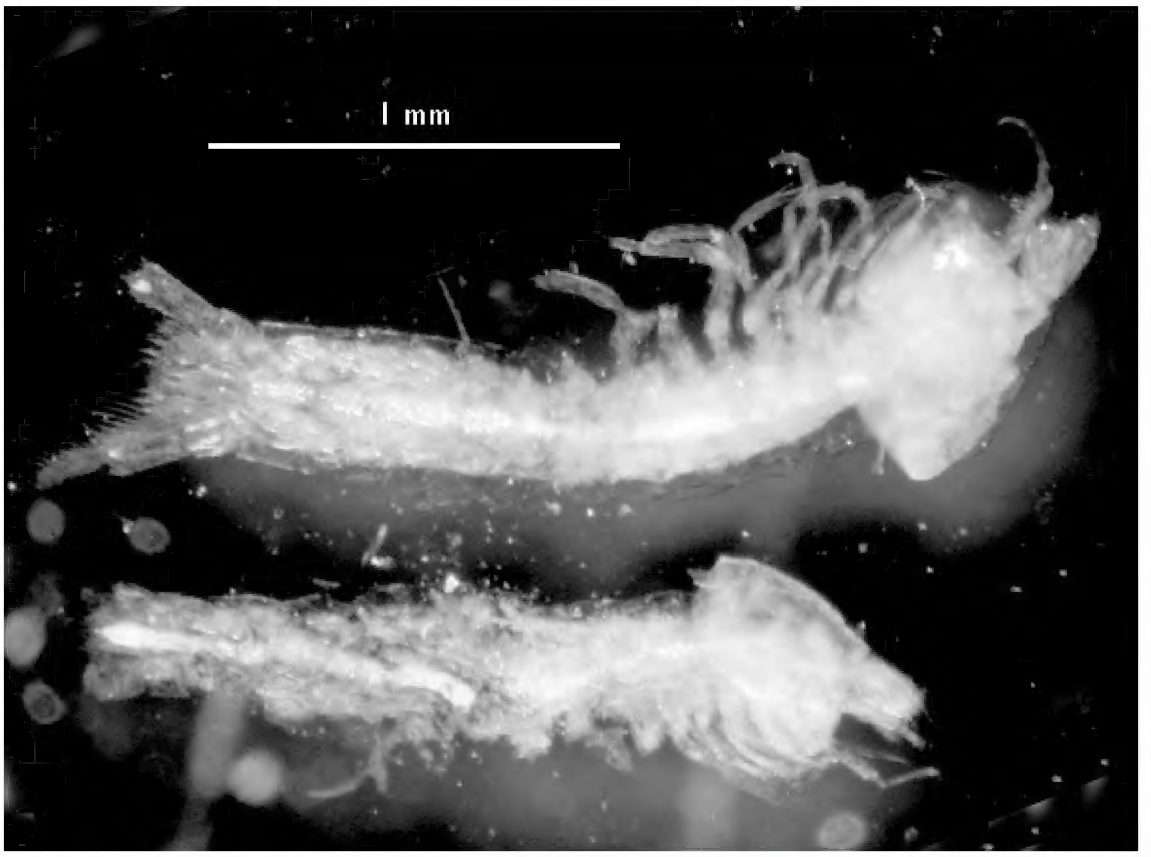

Figure 5. Juvenile *Tethysbaena ophelicola* Wagner (intestine filled with bacteria (?)) (photo N. Ben Eliahu).

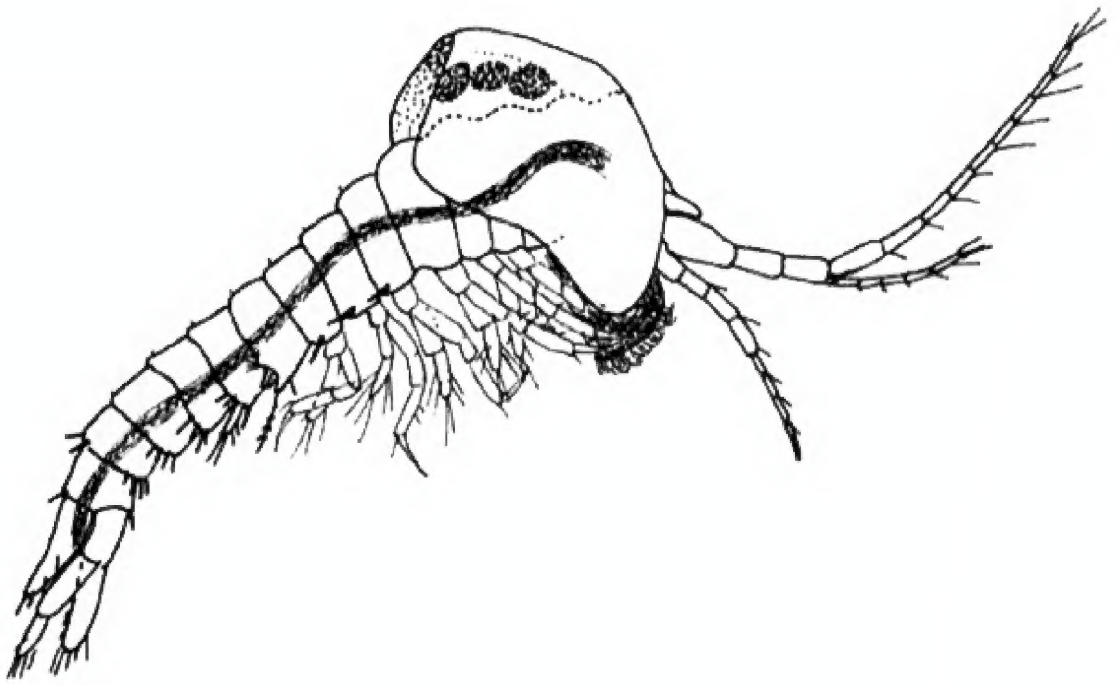

Figure 6. *Halosbaena acanthura* Stock with full intestine (Stock 1976).

Fryer found it strange that this material remained in the intestine in some cases for more than two days. Schram (1986) makes the general statement that the mid gut of the Thermosbaenacea is apparently always loaded with "detritus…the animals dine on". It is possible that we are not dealing with detritus in these pelagic animals, but with bacterial biomass which became unrecognizable in preserved specimens and even in specimens which are encountered or not kept in their natural medium. Only by observing the intestinal filling of live specimens *T. ophelicola* of Ayyalon in their aquatic medium under the appropriate magnification it became clearly visible that it consists of densely packed rounded cells that can represent bacterias.

The affirmation of the symbiotic role of the bacterial filling of the intestinal tract is at this stage purely circumstantial. It is probably similar to what happens in the oceanic alvinellid hot vent worms, where bacteria stored in special trophosomes serve both as food and detoxify sulfide. An even closer comparison would be with certain oligochete and nematode species of the oxygen-deficient and hydrogen sulfide-infested littoral environments which present various degrees of ecto- and endo-symbiosis with sulfur bacteria. In the sulfurous cave lake of Frasassi, Baurmeister et al. (2012) found that the legs of the amphipod *Niphargus itus* Karaman are thickly covered by symbiotic sulfur bacteria. Future microbiological investigations will have to prove the nature of this permanent relationship between *Tethysbaena ophelica* and its bacteria. If positive, it will be the first case of endosymbiosis in the subterranean aquatic medium.

Oviviparity: the crucial synapomorphy

There is surprisingly little mentioning of the thermosbaenacean dorsal brood pouch, its different stages and that of its content in the more recent literature.

The source material at our disposal is in the older works by Stella (1959), and Fryer (1965) on *Tethysbaena argentarii* and by Barker (1962) and Zilch (1972) on *Thermosbaena mirabilis*. The sustained observations of live specimens of *Tethysbaena ophelicola*, in their environment at Ayyalon, and especially the discovery of their supposed bacterial endosymbionts allowed us to use what is known and present an interpretation of the function of the brood pouch, probably the key innovation of the Thermosbaenacea.

The dorsal brood pouch formed by an extension of the carapace of the reproducing female, is no doubt the most singular characteristic of the Thermosbaenacea. It is evident though that in the life history of the sulfide shrimp in its extremely adverse environment, the ovoviviparous development provided by the dorsal breeding pouch, a real marsupium, is a key adaptation for survival.

Dorsal breeding, exceptional among the higher crustaceans, is a consequence of the notonectic positioning of the pelagic Thermosbaenacea in the density interphase. The marsupium with the developing eggs and embryos is protruding-hanging into the anaerobic level, protected from eventual predation. It is however, ventilated with a permanent stream of oxygenated water by the beating maxilliped and pereiopods.

Stella (1955) and Barker (1962) thought that the early embryos reach the pouch freely, being swept in by the aeration current of the thoracal limbs. Zilch (1972), in a detailed work on *Thermosbaena mirabilis*, described how the eggs are transferred to the brood pouch in batches, protected by a membrane (Fig. 7). The membrane is dissolved upon arrival in the pouch. This mode of translocation could perhaps be specific only to this single species in its extremely hot environment.

Several authors mentioned that the eggs and developing juveniles are free in the pouch and "constantly agitated by the inhalant respiratory current" within the liquid content of the pouch (Barker 1962). This observation was confirmed on the Ayyalon species.

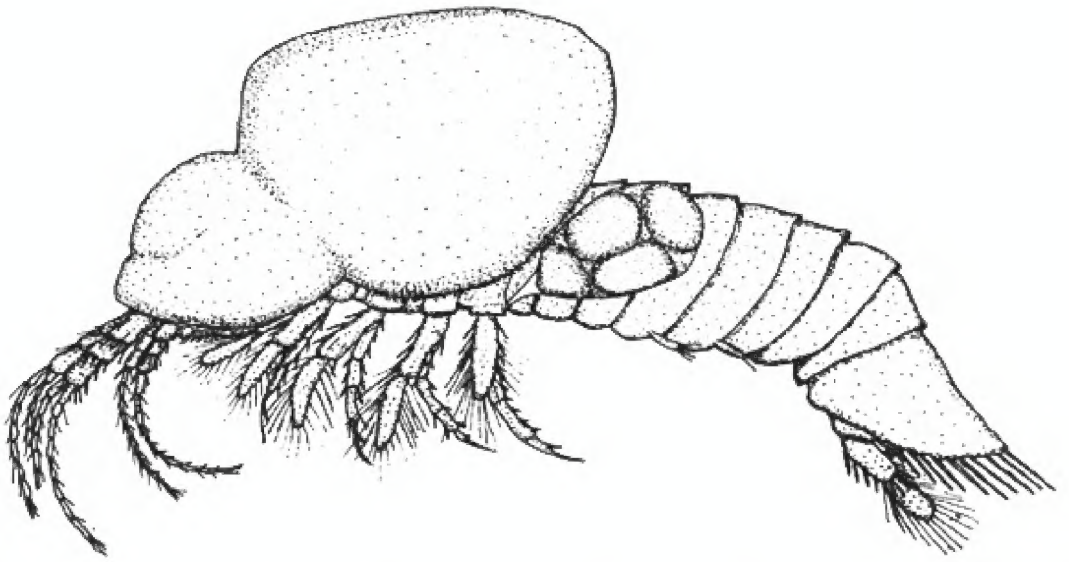

Figure 7. *Thermosbaena mirabilis* Monod. Female, translocating a membrane-protected batch of developing eggs to the brooding pouch (drawing by Zilch 1972).

Figure 8. *Tulumella* sp. from the Bahamas with fullgrown progeny (photo Culver and White 2006).

It seems from the few ovigerous specimens we know that the eggs are large-sized and rich in vitelline matter. Zilch mentions up to 12 embryos in a pouch in *Thermosbaena*. The maximum we saw in *Tethysbaena ophelica* was of 8. As the embryos develop and grow inside the marsupium, their number decreases, most probably due to abortion. A maximum of ovoviviparity was figured in a Caribbean anchialine species of *Tulumella* (Fig. 8), where the marsupium contained an almost ready to be hatched youngster. At least in the assumed typical environment of the Ayyalon pool no seasonality was observed.

The hemolymph lacunae of the cuticular breeding pouch walls were described by Siewing (1958) and by Barker (1962) as especially spacious and in *T. mirabilis* Zilch (1972) describes also some accessory cuticular vesiculated trabeculae emerging into the brooding cavity. The short heart of the thermosbaenaceans is placed immediately below the brood pouch, obviously in the super-order to better serve marsupial circulation

(Wirkner and Richter 2009). Water current is being streamed into the pouch by the beating of the maxillipeds and the anterior thoracopods. The maxillopods themselves are lacune-filled respiratory organs. A favorable micro-environment is probably maintained in the brood chamber by the suction-like current of more oxygenated water from above and by a rich supply of respiratory pigment in the marsupium walls. These are propitious conditions for the development of the embryos of the down-hanging females in the pycnocline. Hydrogen sulfide from the surrounding water is therefore, probably, not much present in the brooding sack medium, since otherwise it would inhibit the development of the youngsters and eventually kill them. The youngsters pass through developmental stages similar to the manca's of the peracarid crustaceans. They leave the brood pouch when they have already functional digestive tract openings. This was evident in the large population of *Tethysbaena ophelicola* of Ayyalon, where the smallest and young hatched specimens already have the intestine filled with bacteria. These accumulated food cells serve most probably also as symbionts which protect the animals against the surrounding hydrogen sulfide toxicity. Without ignoring the other adaptations, the acquisition of this ovoviviparity was decisive in permitting life for the super-order Thermosbaenacea in the pycnoclines of the subterranean waters of the world.

Heat tolerant extremophiles

Monod's *Thermosbaena mirabilis*, "the Marvelous Heat Walker" of Tunisia which lives and reproduces in 42 °C thermal springs (Barker 1962) gave its name and fame to the whole super-order. It is likely the most heat-adapted aquatic metazoan known. The name of the super-order is however somewhat misleading. The animals, as shown, prefer floating and swimming to walking. Schram (1986) indeed wrote that the thermosbaenaceans seem to prefer thermal groundwater. The heuristic example of the Ayyalon population indicates that it would be better to speak of a thermo-tolerance of these crustaceans, and not of a preference.

The rich thermosbaenacean population of the sulfidic pool of Ayyalon lives at a medium temperature of 29.6 °C, which is 5 °C higher than that of the surrounding fresh aquifer (Naaman 2011). The hypogenic artesian groundwaters that are ultimately providing food for these thermosbaenaceans are naturally a few degrees warmer, owing to geothermal heating. Regional tectonism, or exothermic chemical reactions can further contribute to the geothermic warming of the sulfidic deep water. In any case, the pycnocline can have also a sharp thermocline component.

T. relicta (Por) from the Jordan-Dead Sea Valley has also been found at 31 °C, *T. somala* (Chelazzi & Messana) from Somalia at 31 °C and *T. halophila* from Dalmatia is also a thermobiont. The dense populations of *Thethysbaena* found in the often neglected and heavily polluted wells of some Caribbean islands like, as for instance *T. haitiensis* (Wagner 1994) live on "secondary" sulfur bacterial accumulations and do not have to contend with elevated temperatures.

Finally, the thermosbaenaceans can be characterized as limno-euryhaline adapted. They have been reported from water sources which have mineral loads shifting from limnic to mesohaline levels (Wagner 1994). It is evident that in spring outflows or in the pumping devices the salinity interface or halocline, which is another component of the pycnocline, is destroyed and the two originally superposed phreatic waters mix. In the microcosm of the bacteria-rich pycnocline the crustaceans have, however, to face and adapt to radical local changes and fluctuations in dissolved mineral content.

Conclusions

More than half a century has passed since I found in December 1960 my first thermosbaenacean species (Por 1962), and later the paper in which I identified the new subterranean biome Ophel at Ayyalon (Por 2007). Here I propose it to represent the core environment of the Thermosbaenacea. For now I have neither the support, nor the time for further factual and experimental testing of my hypotheses. However, there must be countless aquatic environments like that discovered in Ayyalon, since they supported the evolution of this taxon.

In my opinion, decisive in the evolutionary history of the Thermosbaenacea was their monophagy of sulfur bacteria. From this starting point the entire natural history of the group can be derived as sketched-out above and resumed in the following (Fig. 9).

Thermosbaenaceans are blind, specialized pelagic, bacterial consumers in subterranean stratified standing waters, particularly of sulfur bacteria. Since bacterial chemoautotrophy takes place chiefly in the thin redox and density discontinuity layers, thermosbaenaceans tend to accompany these levels like a kind of upside-down swimming neuston. In response to the radical hydrochemical changes and fluctuations that take place in the thin discontinuity layer (pycnocline), the thermosbaenaceans have developed survival mechanisms to anaerobism, resistance to hydrogen sulfide poisoning, to elevated water temperatures as well as to fluctuating dissolved mineral content. Sulfide is most probably detoxified by intestinal bacteria. All the Thermosbaenacea are ovoviviparus, breeding the offspring in the dorsal marsupium until it acquires its own battery of extremophilic capacities.

With their very specialized life style and its unique morphology, the Thermosbaenacea represent, without doubt, a taxon separate from the Peracarida as considered by the majority of the carcinologists. The dorsal breeding pouch would justify this separation from Peracarida as already suggested by Siewing (1963). Anyhow, as mentioned by Schram (1986) the *lacinia mobilis* of the mandible can no longer be considered as a feature exclusive to the peracarids. Many cladistics analyses also place the Thermosbaenacea as the sistergroup to other peracarid orders (Siewing 1963), which justify its separation from them. However, I suggest not to return to Siewing's "Pancarida", but to maintain Thermosbaenacea for the sulfide shrimp as being a more suggestive name for the group. Besides the Thermosbaenacea, only the

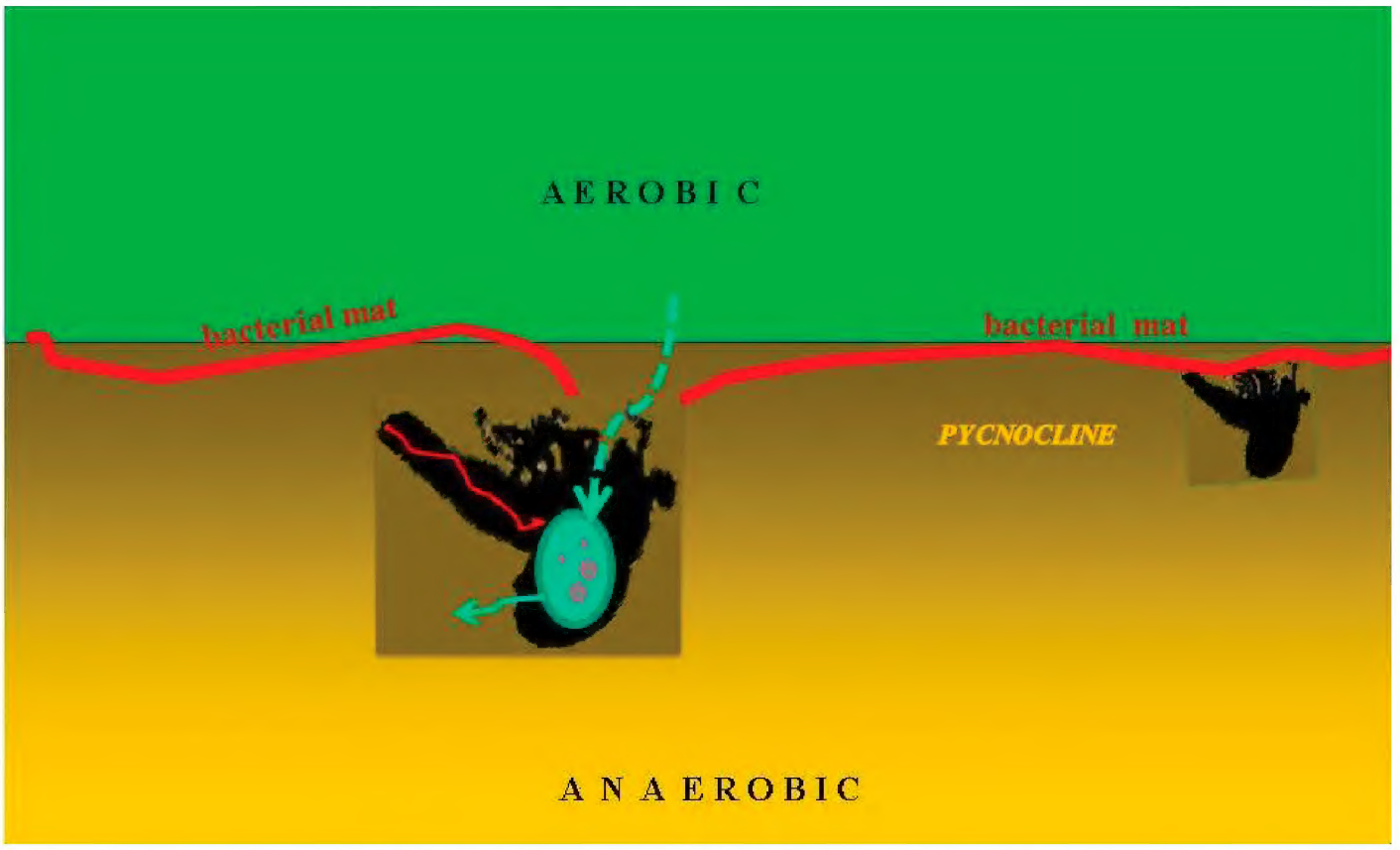

Figure 9. Schematic presentation of the suggested life strategy of a thermosbaenacean (for explanations see text).

copepod *Metacyclops longimaxillis* Defaye & Por is known to live and reproduce in the sulfidic chemosynthetic productive water of the ophiric biome. We do not know anything about their specific adaptation of this cyclopoid to this extreme environment. Only the elongated and setose maxillae which gave the name to the species indicate that it is a primary subterranean bacterioplankton consumer (Defaye and Por 2010).

Biospeleology has been a merely descriptive discipline until recent, since the objects of its study have been only isolated members of allochthonous and truncated ecosystems (Gibert and Deharveng 2002). The ophelic chemoautotrophic system as it appears now in Ayyalon is a firmly established autarchic subterranean ecosystem with its own energy budget and with all the specialized levels, bacterial primary producers and primary consumers like the sulfide shrimp. This is independent from the sunlit biosphere with as yet unfathomed consequences (Por 2011, 2012). Wagner (2012) in his study of *Tethysbaena ophelicola* indeed presents a first hypothetic subterranean chemoautotrophic aquatic food web.

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